



## One herd, different movements: spatial behaviour of female forest chamois in a changing meteorological perspective

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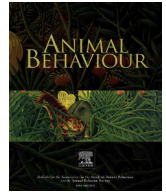
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## One herd, different movements: spatial behaviour of female forest chamois in a changing meteorological perspective

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Mountain herbivores are a multispecies group of animals with behavioural adaptations to the severe living conditions at high elevations. Because of their marked seasonality, mountain ecosystems are particularly sensitive to the impact of long-term meteorological changes. These changes can significantly influence the abundance, distribution, and ultimately the survival of plant and animal species. We focused on the spatial behaviour of a herd of 21 radio-tagged female chamois, *Rupicapra rupicapra*, from December 1998 through November 2001. We investigated home range size, habitat selection and elevational distribution of female chamois. Our findings revealed distinct seasonal patterns in home range size, with smaller ranges observed during the warmer months (May–October), as well as high inter-individual variability in female spatial behaviour, with more than 80% variability in home range size explained by the individual identity. Home range size also decreased with increasing elevations, but only during the warmer months. Sparse larch forests were selected as preferred habitats, shrublands and other coniferous forests were avoided, and grasslands were used proportionally to availability. Chamois were counted yearly in 2000–2001 and from 2020 to 2023 using the same methodology, with a mean temperature increase of  $\sim 2$  °C. Counts revealed an upward shift of up to  $\sim 90$  m in the summer locations of most females, although a minority of groups remained stationary or even moved downwards. Although predation and interspecific competition may have played ancillary roles, alteration in vegetation distribution, and in turn, local food availability, was probably the major factor triggering chamois movements. Contrary to predictions, despite belonging to the same female herd, some individuals showed different spatial behaviour responses, which could be adaptive to ensure survival in case of a changing environmental context, as natural selection can only take place if there is individual variation.

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Mountain environments are strongly seasonal habitats, particularly sensitive to long-term meteorological changes altering the normal course of seasons, with significant consequences on abundance, distribution and eventual survival of plant and animal species (Lovari et al., 2020; Noguès-Bravo et al., 2007; Parmesan, 2006; Schmeller et al., 2022). As the global temperature

increases, its effects are amplified in mountain environments, having relatively greater impacts compared with lowlands (Mountain Research Initiative EDW Working Group, 2015; Pepin et al., 2022), although this pattern could vary with mountain topography (Elsen & Tingley, 2015). Over millennia, mountain-dwelling species must have learnt to cope with fluctuating environments, or they would have gone extinct because of past climatic oscillations. During the last few decades, rising temperatures have been shifting cryophilic (i.e. cold-adapted) plant communities to higher elevations or to cooler pockets (e.g. Gottfried et al., 2012; Parolo & Rossi, 2008; Rammig et al., 2010), due to earlier snow thaw and onset of vegetation regrowth

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(Pettorelli et al., 2007; Rogora et al., 2018). For mountain ungulates, no variation seems to occur at the onset of the rut, which, in turn, does not alter the usual birth season (Lovari et al., 2020; see also Renaud et al., 2019). Thus, the nutritional quality of forage declines earlier, when the young of the year are weaning, which will affect their growth and subsequent winter survival (Dumont et al., 2015; Ferretti et al., 2018; Lovari et al., 2020; Pettorelli et al., 2007; Rughetti & Festa-Bianchet, 2012). Conversely, in several areas, shorter winters have been reported to reduce winter mortality and increase body mass (Brambilla et al., 2024; Jarque-Bascuñana et al., 2022). Thus, the trade-off between costs and benefits of the current thermal change seems to vary between populations, species and local environmental conditions (e.g. elevation and aspect).

Over the last few million years, mountain-dwelling herbivores have evolved morphological, physiological and behavioural adaptations to deal with seasonal variation in weather and in food availability (Cotè & Festa-Bianchet, 2001; Festa-Bianchet, 1988). Warming weather increases heat stress (Semenzato et al., 2021), besides negatively affecting food availability and quality (Ferretti et al., 2018; Lovari et al., 2020; Pettorelli et al., 2007), and intra-specific foraging competition (Fattorini et al., 2023), in turn negatively influencing reproductive success and population dynamics (Chirichella et al., 2021; Lovari et al., 2020; Pettorelli et al., 2007; White et al., 2018). Over the warmer months, heat stress in chamois may occur throughout the 24 h, with a peak in daytime (Carnevali et al., 2016; Grignolio et al., 2018). It has been suggested that forests can act as cooler shelters for mountain ungulates, helping them to partly mitigate the negative effects of increasing temperature (Anderwald et al., 2024; Malagnino et al., 2024; Michaud et al., 2024; Reiner et al., 2021). Furthermore, an elevational increase in forest cover could push mountain ungulates to increase their usage. Females are the main driver of population dynamics (Grignolio et al., 2007), but so far, only one study has suggested that the spatial behaviour of females in forest-dwelling chamois may be particularly affected by environmental warming (Anderwald et al., 2024).

Chamois *Rupicapra* spp. are one of the most iconic and widespread mountain ungulates in Europe and Asia Minor and show behavioural, ecological and physiological adaptations to life at high elevations (Corlatti, Herrero, et al., 2022; Corlatti, Iacolina, et al., 2022; Couturier, 1938). Although there is a wealth of studies on the spatial behaviour and home range size of male northern chamois *R. rupicapra* (e.g. Corlatti, Herrero, et al., 2022; Corlatti, Iacolina, et al., 2022, for a synthesis; Cotza et al., 2023), relevant information for female chamois is still scarce, especially in relation to the effects of the current temperature increase. Furthermore, most research on seasonal variation of spatial behaviour has been based on direct visual observations of individuals marked with plastic collars or ear tags (Boschi & Nievergelt, 2003; Clarke & Henderson, 1984; Kati et al., 2020; Loison et al., 2008; Pachlatko & Nievergelt, 1985). This marking technique is unsuitable for assessing spatial behaviour in low-visibility habitats such as forests and shrubby areas. In particular, out of the only three available studies on habitat selection of female chamois based on telemetry data, only one was based on a substantial sample of radiotracked individuals of this sex (Table 1).

In predator-free or near-free areas, female chamois tend to use higher elevations and have larger home ranges than males to meet energy requirements related to gestation and lactation (Boschi & Nievergelt, 2003; Edelhoff et al., 2023; Filli & Campell, 2006; Nesti et al., 2010; Unterthiner et al., 2012). Females appear to increase their home range size during the warmer months (May–October), when they have sucklings at heel (hereafter, kids) (Boschi & Nievergelt, 2003; Ferrari et al., 1988; Hamr, 1985; Nesti et al., 2010). Kids are born in mid-May to mid-June and start following their mothers a few hours after birth (Krämer, 1969). The relationship between home range size and local habitat richness/selection is well known (Dupke et al., 2017; Lovari, Sforzi, & Mori, 2013; 2017; van Beest et al., 2010; Viana et al., 2018). In the Alps, female chamois tend to select grasslands when snow is absent, as well as larch forests rich in understory food species (Anderwald et al., 2016; Malagnino et al., 2024; Nesti et al., 2010; Unterthiner et al., 2012). Previous studies have also suggested two

**Table 1**

Current knowledge based on peer-reviewed studies on home range size and habitat selection of radio-tagged female northern chamois, *Rupicapra rupicapra*

N tracked females	Home range size	Study period (months)	Selected habitats	Avoided habitats	Source
27	74 ha (warmer months, grid method); and 60 ha (colder months, grid method)	24	NA	NA	Hamr (1985)
17	333 ha (annual, MCP 95)	28	NA	NA	Michallet and Toigo (2000)
6	79 ha (annual, Ker 95); 711 ha (warmer months, Ker 95); and 36 ha (colder months, Ker 95)	34	Open habitats (year)	Scree and scrubs (colder months)	Nesti et al. (2010)
9	56 ha (bimonthly, Ker 95)	24	Larch forest (year) and open habitats (warmer months)	Spruce forest (year), mountain pinewood (warmer months) and scrubs (colder months)	Unterthiner et al. (2012)
30	186.6 ha (annual, MCP 95)	60	NA	NA	Tablado et al. (2016)
50	66 ha (monthly, BBMM 90)	60 (only warm months)	NA	NA	Duparc et al. (2019)
117	132 ha (monthly, Ker 95)	168	NA	NA	Seigle-Ferrand et al. (2022)
9	13.88 ha (monthly, Ker 95)	6 (two autumns)	NA	NA	Edelhoff et al. (2023)
55	NA	156	Forest (warmer months) and open habitats (colder months)	Scree and scrubs (colder months)	Anderwald et al. (2024)
21	81.6 ha (warmer months, Ker 95); and 99.5 ha (colder months, Ker 95)	27	Sparse larch forest	Spruce forest, dense larch forest and rocks	This study

Ker 95: kernel density estimation 95%; MCP 95: minimum convex polygon 95%; BBMM 90: Brownian bridge movement model 90%. NA: not available.

ecotypes of northern chamois, namely 'ridge chamois' and 'forest chamois', based on their primary habitat use (Anderwald et al., 2024; Couturier, 1938). Improving our knowledge on seasonal changes of spatial behaviour, such as home range size, selection of habitat types and elevational belts by forest-dwelling female chamois, could help us understand how changing weather conditions and available habitats will affect future responses of mountain ungulates (Corlatti, Herrero, et al., 2022; Seigle-Ferrand et al., 2021). Furthermore, no information is available on individual variations of ranging movements among female chamois belonging to the same herd, presumably exposed to the same environmental and social determinants (Duranton & Gaunet, 2016; Ward & Webster, 2016). If so, consistent behaviour across individuals could be expected. In fact, behaving as the majority of group members should determine greater survival success, whereas variability at the individual level could provide survival alternatives to the main tactic (Del Mar Delgado et al., 2018). This argument is potentially important to explain the spatial reactions of herbivores to ongoing meteorological change, which is already leading to alterations in the spatial distribution of mountain species, especially chamois (Lovari et al., 2020; Semenzato et al., 2021).

We have investigated short-term seasonal variations in home range size and habitat selection of individual forest-dwelling female chamois belonging to the same herd in an Alpine protected area using intensive very high frequency (VHF) radiotracking and direct observations. We have defined 'herd' as the chamois attending the same valley, showing overlapping home ranges with variable groupings (cf. Krämer, 1969). Although home range reflects the amount of space used by an individual, habitat selection mirrors the degree of preference in the environmental characteristics of the space used. Therefore, both aspects are tightly linked and jointly contribute to the understanding of animal spatial behaviour. Furthermore, we have assessed the effect of kid presence in the early suckling stages on the female's home range size. Finally, we compared official counts conducted in 2000–2001 with those in the period from 2020 to 2023 to assess long-term differences in the spatial distribution of the same chamois herd. We predicted that (1) in the colder months (November–April), female chamois should move to snow-free areas, thus avoiding alpine pastures (Krämer, 1969); (2) home ranges of adult female chamois would be smaller during the colder months, when feeding areas are limited because of snow cover and juveniles are no longer heavily dependent on mothers; and (3) there would be little variation in the spatial behaviour (i.e. home range size and elevation usage) of females belonging to the same group (Duparc et al., 2019; Ward & Webster, 2016).

## METHODS

### Study Area

Our study was conducted in the Paneveggio–Pale di San Martino Natural Park, in the eastern Italian Alps (hereafter PNP; 46°30' N–11°45' E; 19,710 ha, elevation: 1465–2330 m a.s.l.; radiotracking period: 1999–2001; chamois counts: July 2000–2001 and from 2020 to 2023). Chamois were trapped (see below) in the central-southern part (7700 ha) of the Cavallazza area. Most (31%) of the study area was covered with alpine grasslands and peat bogs, including *Nardus stricta* L., *Festuca varia* Haenke and *Deschampsia caespitosa* (L.) Beauv. It was located below a steep, rocky area (13%), and above a dense, shrubby, steep slope (5%) with *Alnus glutinosa* (L.) Gaertn., *Juniperus communis* L. and *Rhododendron ferrugineum* L. Conifer forest also occurred, which included dwarf mountain pines, *Pinus mugo*, Turra (4%), sparse (9%) and dense (20%) larch,

*Larix decidua* L. patches, and a spruce, *Picea abies* (L.) H. Karst forest (18%). Thus, the study area contained a mosaic of seven macrohabitats, which allowed their selection by chamois.

The local climate is prealpine-continental, with snowy winters and mild summers (Carnevali et al., 2016). During our study period, weather data recorded at the Passo Rolle station showed that February was the coldest month (mean T: −4.5 °C), whereas August was the warmest one (mean T: 10.5 °C). The warmer semester occurred from May through October (mean T ± SD = 7.4 ± 1.3 °C), whereas the colder one was from November through April (mean T ± SD = −2.6 ± 1.2 °C; Carnevali et al., 2016). Annual precipitation was 1110 mm, peaking in October (185 mm). Most snow fell in late winter-early spring (January–April), when the monthly average snow depth ranged from 40 to 170 cm.

Our study population of chamois can be considered as forest-dwelling (sensu Baumann & Struch, 2000), i.e. mostly observed in covered habitats (conifer forests and shrubland: Guastella, 2001). The local population density was ~19 individuals/100 ha, with a female density of 10.1–15.8 ind./100 ha (Fattorini et al., 2007). Other wild ungulate species included red deer, *Cervus elaphus* (~6 ind./100 ha), at lower elevations, below the chamois area, whereas roe deer, *Capreolus capreolus*, were rarely observed within the chamois range (Mattedi et al., 1997). Since our radiotracking study, red deer have increased in numbers and have slowly spread to higher elevations. Golden eagles, *Aquila chrysaetos*, prey mostly on juveniles (Bertolino, 2003) and occasionally on adult chamois (Lovari, 1977), but no large terrestrial carnivore was present at the time of our radiotracking work. No hunting was allowed in our study area, a state property reserve since 1982. Human disturbance was limited but increased in the warmer months, whereas livestock presence was mainly concentrated around farmhouses ('malghe'), just out of our study area (Monaco, 2003).

### Chamois Captures and Radiotracking

We used large box traps, baited with salt, to catch chamois ( $N = 23$  sexually mature, i.e. >2 years old, females; representing ~40% of the local female herd), during late May–mid July, in 1999–2001. Cage traps (1.70 × 1.50 × 2.50 m) were built at capture sites, adapting them to cliff morphology and using wooden planks and other natural materials (rocks, branches and trunks) found on site (a trapping method commonly used for chamois: Appolinaire et al., 1984). At the bottom of the inner portion, zootechnical salt was placed as an attractant, and a dropping net was positioned at the entrance. After the chamois entered the trap, from a distance, an operator activated the triggering mechanism, i.e. a small piston releasing the net door and causing it to fall. The chamois, in an attempt to escape, would get entangled in the net. When activated, traps were checked for the entire period of daily triggering (from dawn to dusk) by a team of at least 2–3 people (including a veterinarian) to release the net when the chamois was inside. Upon that, in less than 15 min, the team reached the animal, checked its health conditions, ear-tagged it and fitted a VHF radio-collar (TXH-3—Televilt, Inc., Sweden). To allow identification, an individual-specific code was defined by using colours of the ear tags (red and yellow) and those of the radio collars (yellow and white), as well as by glueing and sawing coloured plastic bands (blue, red and black) to the latter. As captures involved individuals of different ages, radio collars were fitted to allow for the growth of chamois necks.

We wished to radio-tag about 50% of the local herd in a relatively short time to be able to monitor them under the same environmental conditions. After catching 23 females, the trade-off between costs (labour and time) and benefits (new chamois caught) strongly suggested stopping new catching attempts. In

fact, repeated recaptures of the same individuals would increase useless risks. The age of chamois was determined through horn ring counts (3–15 years: Couturier, 1938; Schröder & von Elsner-Schack, 1985). Throughout the study period, the mean  $\pm$  SD age of monitored chamois was  $8.3 \pm 3.8$  years (median 8.7 years; range 3–14.5 years). Before data collection began, the mean location error was determined by positioning five radio tags in 200 known locations/operator at ground level and by calculating the difference between actual and estimated locations (mean  $\pm$  SD =  $27.2 \pm 5.5$  m). Fixes collected in the first week from radiotagging were discarded from our analyses to prevent bias due to the novelty of the radio collar. To calculate the borders of the study area, we defined a total of 100% minimum convex polygon (MCP) encompassing all radiolocations, plus a 200 m wide buffer area (Castillo et al., 2012).

The data collection system remained constant throughout the whole research period (December 1998–November 2001). We used discontinuous radiotracking, locating an animal at regular time intervals (see below), by triangulation (Kenward, 1987). Our goal was to obtain at least 20 fixes per month for each chamois. The 24 h period was divided into three time slots of 8 h each so that each slot consisted of the same number of fixes/months, and each fix was 4 h from the others to limit autocorrelation (Grignolio et al., 2007). Our study area had good sealed and dirt road coverage, and when in doubt, checks on foot were made to overcome challenging topographic features for signal location. We never went so close to chamois to elicit their escape reaction. After each field session, fixes (3–5 bearings for each fix) were recorded on a map. The elevation and habitat type where each individual was located, together with the coordinates of each fix, were entered into a data set. An error polygon was identified on the map, with its centroid assumed to be the actual location of the animal (fix), defined by a pair of XY coordinates (Kenward, 1987). The measure of the linear distance from the centroid to the farthest vertex represented the radius of the confidence circle, whose area depended on the error arc, the intersection of the angles, and the distance between the animal and the observer (Bartolommei et al., 2012). Only polygons with a vertex-centroid distance lower than 50 m were considered reliable (Bartolommei et al., 2012). Positions confirmed by direct sightings were considered error-free. In total, 12 906 locations of females were collected, of which approximately 31% were confirmed within 1 h by direct sightings.

Together with direct sightings during radiotracking bouts, further observations were conducted during the warmer months ( $\sim$ 187 h/year) in each study year to identify collared females with offspring from those without kids. Female alpine chamois (life expectancy:  $>20$  years; Corlatti, Herrero, et al., 2022) are known to maintain frequent close contact with their offspring throughout lactation (Ruckstuhl & Ingold, 1999). We identified females with kids (one, rarely two, per female: Corlatti, Herrero, et al., 2022) when female-juvenile pairs were sighted alone or, when observed within groups, they were the closest individuals to each other in most observations, especially when lying down (Ruckstuhl & Ingold, 1999), as well as when nursing.

Among the 23 female chamois captured and radiotracked, one died within 1 month from capture, and one showed home ranges  $\sim$ 250% larger than the mean home range of the other females in all seasons, together with  $\sim$ 70% smaller overlap with other individuals than the mean overlap, suggesting an out-group spatial behaviour. Data from these individuals were not used for analyses to improve consistency and reliability. All results have been based on data from 21 females monitored for a mean  $\pm$  SD of  $27 \pm 9$  consecutive months.

### Ethical Note

The trapping of chamois was conducted by park personnel in full compliance with Italian regulations, as authorized by the Italian Ministry of Environment and approved by ISPRA ('Istituto Superiore per la Protezione e la Ricerca Ambientale') under protocols 017 853 and 002 2988. No ethical approval from a local animal welfare committee was sought as it was not required. Trapping was executed by park personnel under continuous veterinary supervision, using traps baited with salt licks. During the weaning period, chamois form nursery groups and juveniles are not always in proximity to their mothers. As a result, temporary separations exceeding those caused by capture and handling naturally occur in this species (Ruckstuhl & Ingold, 1998). Once trapped, female chamois were handled within 30–45 min by a team of skilled handlers coordinated by park staff. To minimize stress, each animal was restrained immediately upon handling, its eyes covered to reduce anxiety, and its legs securely bound to prevent injuries. Every effort was made to reduce the procedure time, limiting individual handling time to approximately 15–20 min, and allowing for a rapid on-site release. Young of the year and their mothers were released simultaneously to prevent separation. Throughout the study, 23 individuals were captured, with no injuries or fatalities caused by the trapping and handling. All capture, handling and sampling procedures adhered strictly to national animal welfare laws and the ethical guidelines outlined in ISPRA accreditations, in line with Italian National Law 157/1992, Legislative Decrees 196/2003 and 26/2014, European Regulation 2016/679, and the European 'Habitats' Directive 92/43/EEC. GPS collars weighed  $\sim$ 500 g, i.e. much less than 2.5% of the animal's body mass, and were fitted exclusively on adult individuals. To accommodate potential seasonal fluctuations in neck circumference, an approximate 2 cm gap was left between the collar and the neck, ensuring that the device remained secured without excessive movement. Postcapture observations revealed no apparent alteration in the chamois behaviour, nor any evidence of long-term effects. Behavioural monitoring was conducted from a distance to minimize disturbance. Furthermore, no adverse consequences, such as injuries or disruptions of daily activity, were associated with collar use.

### Home Range Estimation

For each individual, the overall, seasonal, and bimonthly home range sizes were estimated through both 95% and 50% fixed kernel (Ker 95% and Ker 50%, respectively; the latter also known as 'core area'), as well as through 100% and 95% MCP. Although MCP is suitable for a basic description of habitat selection, fixed kernel home range estimates provide a more accurate picture by discarding the peripheral unused areas (Burgman & Fox, 2003). The overall home ranges considered all fixes collected throughout the monitoring period, the seasonal (semestral) timescale considered fixes collected within the warmer and colder months (respectively May–October and November–April; cf. Carnevali et al., 2016, from the same study area and period), whereas the bimonthly temporal scale considered fixes collected within six bimesters, defined according to the weather variability in our study site and the biological cycle of female chamois (January–February; March–April; May–June; July–August; September–October; November–December). Home range estimation was performed in R version 3.3.1 (R Core Team, 2013), using packages *ade4* (Dray & Dufour, 2007), *adehabitat* (Calenge, 2006), and *HRTools* (Preatoni & Bisi, 2013). The last package was also used to assess the home range

(Ker 95%) overlap between each pair of individuals monitored at the same time (interindividual overlap, quantified through the Minta index, on a 0–1 scale; Minta, 1993), and the home range overlap of the same individuals in different years (interannual overlap, quantified as %), which were calculated by considering the overall home range of each female over the monitoring period. These indices were calculated to inform on the degree of space sharing between members of the same chamois herd. As to the 95% and 50% fixed kernel estimates, we used an ad hoc smoothing parameter ( $h_{\text{adhoc}}$ ) to prevent oversmoothing or undersmoothing (Berger & Gese, 2007).

#### Statistical Analysis: Home Range Size

We investigated variation in the sizes of the bimonthly home ranges (Ker 95%) and core areas (Ker 50%) of female chamois (considered as the averages throughout the study years, for each individual) according to seasonality, chamois age and elevation through generalized additive mixed models (GAMMs; Wood, 2017). Although our primary interest was to evaluate seasonal variations, chamois age (range: ~3–15 years) and elevation (range: ~1700–1900 m a.s.l.) were also considered as potential predictors driving the sizes of the home range and core area of chamois. In particular, age may affect energy requirements, as well as be a proxy for the experience of individuals in moving across the area, promoting knowledge of important information, e.g. shelter and best food patch locations, thus influencing home range size (Brambilla et al., 2006; Levet et al., 1995; Monaco, 2003). Because of the conical shape of mountains, at higher elevations, the space available to individuals is reduced with respect to lower areas (White et al., 2018). Quality and distribution of mountain vegetation are also influenced by elevation (Lovari et al., 2020), thereby shaping herbivore movements. Thus, we considered all the above predictors in an initial scrutinizing model (see below).

The flexibility of GAMMs allowed us to evaluate potential nonlinear relationships of age and elevation with our response variables through nonparametric smoothing functions. Models were fitted using the R package *mgcv* (Wood, 2017). Both response variables were ln-transformed to improve the homogeneity of residuals and modelled through a Gaussian error distribution (link function: identity). The female chamois identity was included as a random factor with smoother linkage to account for multiple home range size estimates calculated on the same individual every bimester. We included the bimester as a parametric predictor (categorical; reference level: January–February) and two predictor variables, which were modelled through natural cubic spline functions: age (continuous, in years; considered as the median age of each female over its monitoring period, to the nearest 0.5 year) and elevation (continuous, in m a.s.l.; as the mean elevation at which each female was located in the relevant bimester). Both age and elevation were included as interactions with the bimester to investigate whether their effects are bimester-dependent.

For both response variables, we conducted an all-subset model selection (Harrison et al., 2018) to investigate the support of all the possible combinations of predictors in influencing home range and core area sizes of female chamois. We scrutinized any possible combination of predictors, each one representing a candidate model underlying a specific a priori hypothesis (including the hypothesis that home range variation is solely due to interindividual variation as reflected by the null, random intercept-only model), because none of them could be discarded in advance. This approach is recommended when prior knowledge of the investigated phenomenon is not strong enough to force predictors in the model (Stephens et al., 2005), as in our case, where age and elevation might be possible drivers, but no specific information on

chamois in our study area is available. The model selection was based on the Akaike information criterion corrected for small samples (AICc), with the random factor included in all candidate models, and was performed using the R package *MuMIn* (Bartoń, 2023). The difference between the AICc of each candidate model and the AICc of the model with the lowest AICc, namely  $\Delta\text{AICc}$ , was considered for model ranking. Only models that had  $\Delta\text{AICc} < 2$  were selected and, among them, any model whose AICc was higher than that of a simpler nested alternative was excluded to avoid retaining overly complex models (nesting rule: Harrison et al., 2018). Because only a single model was selected for each response variable (cf. Results), only that was used for inference on the effects of predictor variables, with no need to perform model averaging or separate inference from different selected models. To evaluate differences between bimonthly estimates of home range and core area, as the bimester was a parametric predictor, we computed estimated marginal means (R package *emmeans*; Lenth, 2023) and performed post hoc pairwise comparisons between all bimesters by correcting *P* values for multiple comparisons through the single-step method (R package *multcomp*; Hothorn et al., 2008). Then, we estimated the adjusted repeatability (Stoffel et al., 2017) within the same female chamois in the bimonthly (ln-transformed) home range and core area sizes while accounting for the fixed effect of the predictor supported in the best model (i.e. the bimester, cf. Results), in a linear mixed model framework. This metric quantifies the variability in home range and core area explained by the individual identity, after controlling for the effect of bimester. Thus, this evaluation provides information on individual heterogeneity in the spatial extent used by female chamois. Higher values of repeatability would suggest that home range and core areas show substantial interindividual variation in spatial behaviour, emphasizing behavioural diversity between members of the same herd. Repeatability, relevant uncertainty and significance were estimated using the R package *rptR* (Stoffel et al., 2017), with 10 000 bootstrap replicates and a likelihood ratio test, using the home range and core area sizes as response variables, the bimester as a fixed effect as supported by the selected model (cf. Results), and female chamois identity as a random intercept (repeated measures per female:  $N = 6$  for 17 females;  $N = 4$  for 3 females; and  $N = 3$  for 1 female).

In a second step, we investigated potential nonlinear variations in the bimonthly home range and core area sizes of female chamois according to the elevation, separately for each bimester. This analysis nullifies the effect of seasonality (bimester), which may mask other effects, thus providing more detailed information on the potential role of elevation compared with the first-step analysis. Having one estimate of home range/core area per female, we fitted a generalized additive model (GAM) for each bimester. As in the previous step, we included the mean elevation as a smooth term (natural cubic spline) and modelled both (ln-transformed) response variables with a Gaussian error distribution (link: identity). Model selection was therefore performed separately for each bimester and conducted as above to investigate the potential role of elevation in affecting the home range/core area of female chamois against a null model (i.e. a model not including elevation, as the elevation was the only predictor variable). As the model comparison involved solely a model with elevation against the null, intercept-only model, a likelihood ratio test was also performed to assess whether elevation significantly contributed to explaining differences between models.

In the third step, we assessed the differences in the year-specific home range and core area sizes between females with and without kid(s) during the early-nursing stage (May–June bimester) while still accounting for the potentially nonlinear effect of elevation. We fitted two GAMMs and modelled both (ln-

transformed) response variables with Gaussian errors (link: identity). Having multiple estimates of home range/core area for each female and each study year, we included the chamois identity and the study year as random factors. Kid presence was included as a parametric predictor (reference level: kid absent), and the elevation was modelled as a smooth term (natural cubic spline). Model selection was performed as for the first step, i.e. while retaining the two random factors in all candidate models. In all steps, the best models were checked through visual inspection of residuals and assessment of model fit.

### Statistical Analysis: Habitat Selection

Two habitat selection analyses were performed separately to investigate preference, avoidance, or proportional use (no selection) of the various habitat types and elevational belts by female chamois. Individual-based selection of habitat types was assessed by comparing the proportion of habitat used by each female chamois against the available proportion of the same habitat at two different scales (second-order selection: percentage of habitat within the home range vs percentage of habitat within the study area; third-order selection: percentage of female locations observed within the habitat vs percentage of habitat within the home range; Johnson, 1980). For the elevation, only a second-order selection was performed by considering the percentage of female locations observed within the elevational belt vs the percentage of the elevational belt within the study area. We used the nonparametric method by Fattorini et al. (2014). For each habitat type or elevational belt, we assessed whether it was proportionally used according to its availability using the sign test based on the number of female chamois for which the proportion of use exceeded the proportion of availability. Then, the *P* values resulting from each single test were combined for assessing the overall hypothesis of proportional use through a permutational procedure

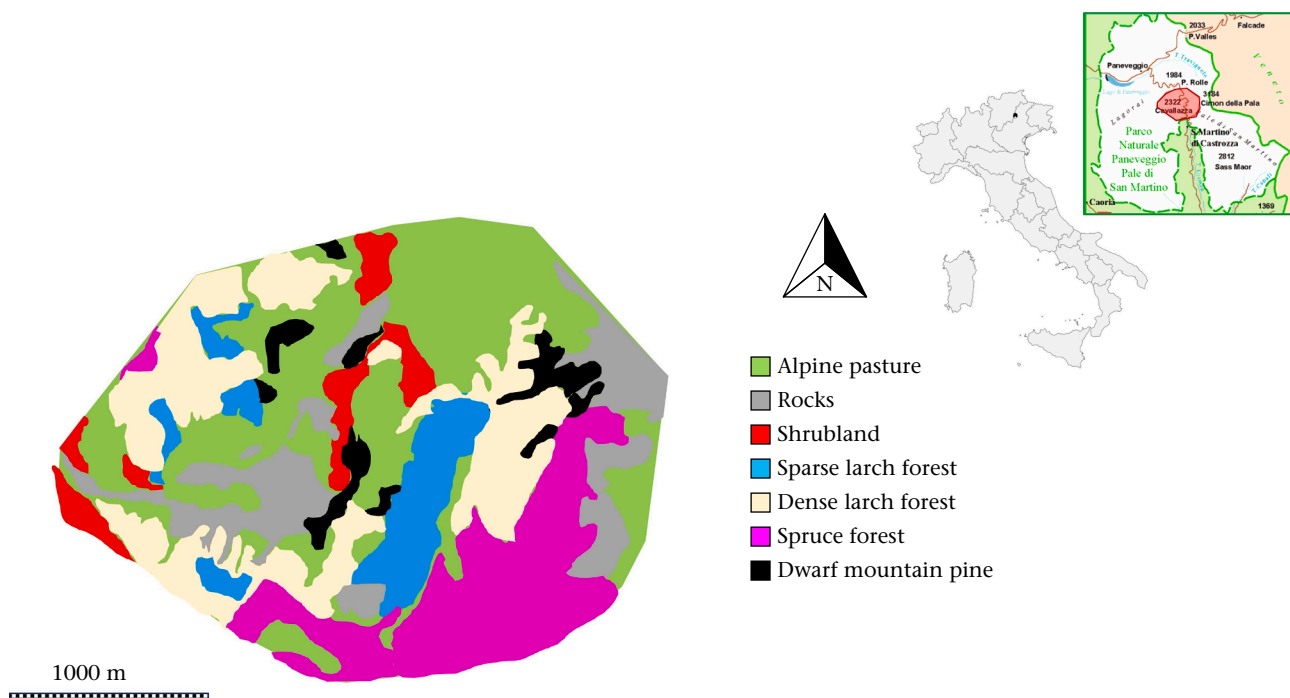
(where we estimated the permutation distribution using a random sample of 100 000 sign choices), giving rise to an overall *P* value (Fattorini et al., 2014, 2017).

As to habitat *sensu stricto*, we considered the seven main types occurring in the study area: alpine pasture, rocks (i.e. cliffs and screes), shrubland, sparse larch forest, dense larch forest, spruce forest and dwarf mountain pine scrubwood (Fig. 1). Concerning elevation, we considered seven belts: (1) <1700 m a.s.l.; (2) 1701–1800 m a.s.l.; (3) 1801–1900 m a.s.l.; (4) 1901–2000 m a.s.l.; (5) 2001–2100 m a.s.l.; (6) 2101–2200 m a.s.l.; (7) >2200 m a.s.l. Testing was conducted through the package *phuassess* (Fattorini et al., 2017) in R 3.3.1, with the significance level set at 0.05. Analyses were conducted separately for each semester and bimester (see 'Home range estimation' for temporal criteria).

### Statistical Analysis: Bidecadal Changes in Chamois Terrain Use

We investigated bidecadal (~20 years) differences in the environmental characteristics (elevation, slope, aspect and rock cover) of the locations of female chamois sightings (with male sightings, for an intersexual comparison) recorded during standardized block counts conducted by operators from the Natural Park and the Provincial Forestry Agency (Berduco & Besson, 1982) in mid-July 2000–2001 (period A) and 2020–2023 (period B). Although a comparison between two time periods does not permit drawing definite conclusions on long-term trends or evolutionary adaptations, it can suggest options available to individuals of the same subpopulation, providing a clue for understanding chamois movements.

We considered male and female groups of chamois separately for analyses. The same counting method (block count locations, operator number, same optics, same week in July and same time of day) was used each year in 2000–2001 and 2020–2023. Operators recorded the numbers and sex/age classes of chamois for each



**Figure 1.** Habitat type composition of the study area (Paneveggio-Pale di San Martino Natural Park, Northern Italy). Inset: broader location of the study area (red line shows the Cavallazza area).

sighting and georeferenced them. Details on block counts and statistical analyses are reported in the Supplementary Material.

## RESULTS

### Home Range Size

The mean  $\pm$  SD overall home range of female chamois was  $90.1 \pm 49.1$  ha (Ker 95%; MCP 95%:  $133.1 \pm 80.9$  ha; MCP 100%:  $217.3 \pm 104.1$  ha), whereas the core area (Ker 50%) was  $15.1 \pm 8.6$  ha. Both home ranges and core areas were larger during the colder season than in the warmer one (mean  $\pm$  SD; warmer: Ker 95%,  $81.6 \pm 50.3$  ha; Ker 50%,  $13.9 \pm 6.9$  ha; colder: Ker 95%,  $99.5 \pm 58.2$  ha; Ker 50%,  $17.6 \pm 7.8$  ha). The interindividual overlap between home ranges of female chamois throughout their monitoring period, weighted by the number of different individuals against which the overlap of each female was assessed, was  $0.48 \pm 0.20$  (weighted mean Minta index  $\pm$  weighted SD; range 0.24–0.62). The mean  $\pm$  SD interannual overlap of the same individual, respectively in home range and core area, was  $70\% \pm 18\%$  and  $58\% \pm 25\%$  (first vs second monitoring year;  $N = 8$  individuals),  $67\% \pm 18\%$  and  $53\% \pm 22\%$  (first vs third monitoring year;  $N = 7$  individuals) and  $75\% \pm 16\%$  and  $63\% \pm 18\%$  (second vs third monitoring year;  $N = 14$  individuals).

For both the bimonthly home range and the core area sizes, a single best model with considerable support over other candidate models ( $\Delta$ AIC > 10) was selected, explaining > 80% data variability (adjusted  $R^2$ , home range 0.82; core area 0.84) and including only the effect of the bimester (Tables S1–S2). Therefore, age and elevation were not supported as influential predictors of bimonthly home range and core area sizes of female chamois. We found that home ranges were the smallest in May–October and increased in November–April (Table 2; Fig. 2a). Core areas tended to follow the same seasonal pattern (Fig. 2b; Table 2). Repeatability ( $R$ ) within the same individual was always high and significant (home range:  $R = 0.825$ , 95% CI: 0.674–0.900,  $P < 0.0001$ ; core area: 0.821, 95% CI: 0.672–0.897,  $P < 0.0001$ ), reflecting substantial interindividual variability in female spatial behaviour. This means that, while accounting for the effect of bimester, >80% of the variability in home range size was explained by the individual identity.

When we investigated the effect of elevation separately for each bimester, we found that the elevation was an influential predictor only in the warmer months, with consistent results

obtained by model selection and null hypothesis testing (Tables S3–S4). In particular, from May to October, home ranges of female chamois tended to decrease with increasing elevation (Table S6; Fig. 3a–f). Core areas followed a similar pattern, decreasing at higher elevations only in March–April and from July to October (Table S6; Fig. 3g–l). In these months, the elevation explained ~25%–52% of the variability in the home range and core area size, depending on the bimester (Table S6).

When we compared variations in home range and core area sizes of females with and without kids during the early-lactation period (May–June), we found that a single best model was selected (Table S5), explaining most of the data variability (adjusted  $R^2$ , home range 0.99; core area 0.98) and including only the effect of the elevation (Table S7). Thus, kid presence was not found to be a predictor variable.

### Habitat Selection

At both the second and the third levels of selection, in all the bimonthly periods as well as at the semester level, there was strong evidence that female chamois did not use habitat types and elevational belts proportionally to their availability overall ( $P < 0.0001$  in all cases). Among habitats, chamois positively selected the sparse larch forest year round and consistently avoided almost all the others, except alpine pastures, which were used in proportion to their local availability throughout the year (Table S8; Fig. 4a). The dwarf mountain pine scrubwood was also used in proportion to its availability in the colder semester, at the second order of selection, and throughout the year, at the third order of selection, as well as the shrubland was during July–December, at both orders of selection (Table S8; Fig. 4a). In terms of elevation, chamois selected the 1701–1800 m and 1801–1900 m belts throughout the year, although the latter was used proportionally to availability between November and February (Table S9; Fig. 4b). Elevations below 1700 m and above 1900 m were always avoided, except for the 2101–2200 m belt in July–August, which was used in proportion to its availability (Table S9; Fig. 4b).

### Bidecadal Change in Chamois Terrain Use

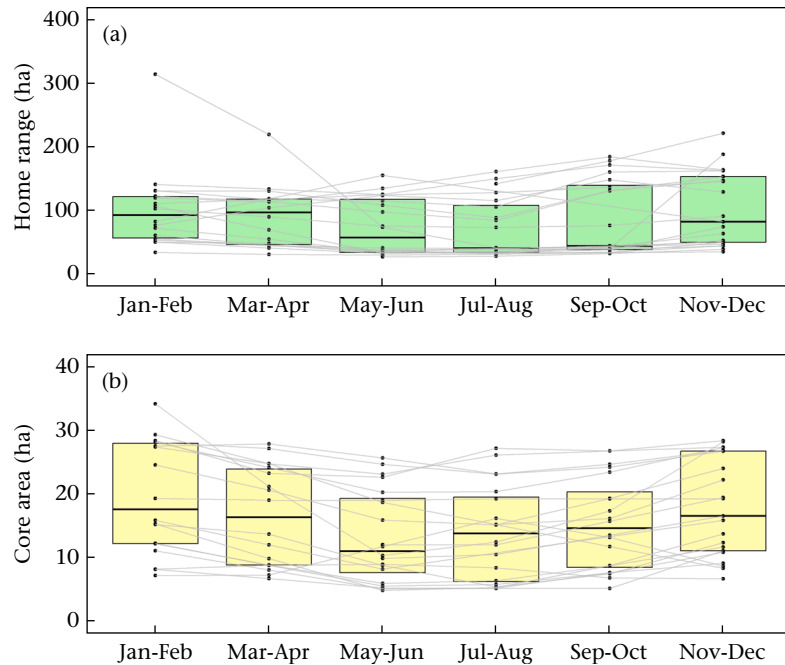
Over the last two decades, July temperatures in our study area have increased by ~2 °C, with a mean rate of ~0.1 °C/year (Supplementary Material; Fig. 5b). In the same period, male and female sightings of chamois during standardized block counts

**Table 2**

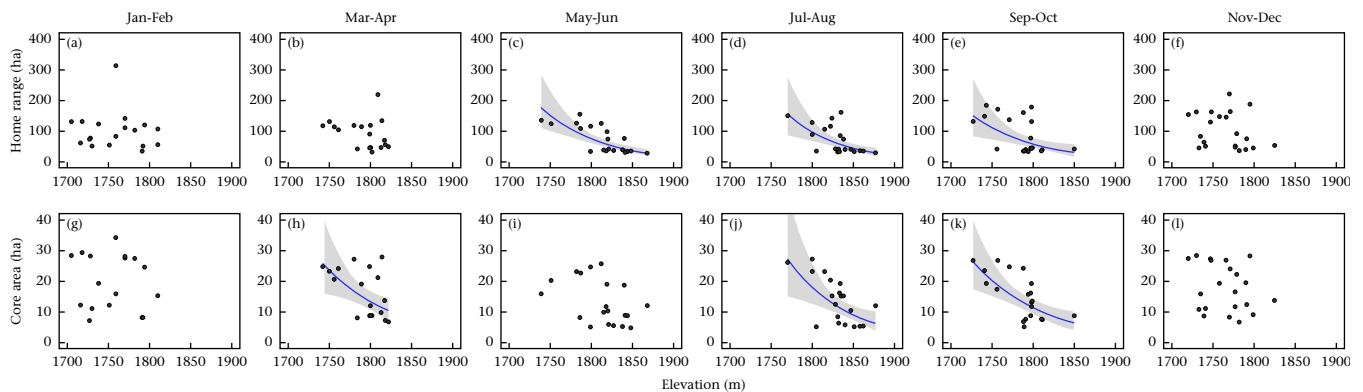
Post hoc pairwise comparisons testing differences in home range and core area of female chamois between bimesters

Post hoc comparison	Home range		Core area	
	Coefficient (SE)	<i>P</i> -value	Coefficient (SE)	<i>P</i>
January–February vs March–April	0.095 (0.085)	0.869	0.179 (0.073)	0.153
January–February vs May–June	0.286 (0.083)	<b>0.011</b>	0.427 (0.072)	<b>&lt; 0.001</b>
January–February vs July–August	0.351 (0.084)	<b>&lt; 0.001</b>	0.389 (0.073)	<b>&lt; 0.001</b>
January–February vs September–October	0.199 (0.084)	0.178	0.261 (0.073)	<b>0.007</b>
January–February vs November–December	–0.005 (0.083)	1.000	0.073 (0.072)	0.908
March–April vs May–June	0.191 (0.083)	0.211	0.248 (0.072)	<b>0.011</b>
March–April vs July–August	0.255 (0.084)	<b>0.036</b>	0.210 (0.073)	0.053
March–April vs September–October	0.103 (0.084)	0.821	0.082 (0.073)	0.867
March–April vs November–December	–0.100 (0.083)	0.830	–0.106 (0.072)	0.677
May–June vs July–August	0.064 (0.081)	0.968	–0.038 (0.070)	0.994
May–June vs September–October	–0.087 (0.081)	0.891	–0.166 (0.070)	0.182
May–June vs November–December	–0.291 (0.080)	<b>0.006</b>	–0.354 (0.069)	<b>&lt; 0.001</b>
July–August vs September–October	–0.152 (0.081)	0.422	–0.128 (0.070)	0.452
July–August vs November–December	–0.355 (0.080)	<b>&lt; 0.001</b>	–0.316 (0.069)	<b>&lt; 0.001</b>
September–October vs November–December	–0.203 (0.080)	0.121	–0.188 (0.069)	0.081

Coefficients, standard errors (SEs) and *P* values adjusted for multiple comparisons are reported. Significant ( $P < 0.05$ ) comparisons are bolded.



**Figure 2.** Bimonthly individual variation in the size of (a) home range and (b) core area by female chamois, *Rupicapra rupicapra* (black dots connected by grey lines). Horizontal line: median; box: first and third quartiles. Bimesters were defined according to the weather variability in our study site and the biological cycle of female chamois (colder months: November-December, January-February and March-April; warmer months: May-June, July-August and September-October).



**Figure 3.** Bimester-specific relationships between the elevation (metres a.s.l.) and sizes of the (a-f) home range and (g-l) core area, in female chamois, *Rupicapra rupicapra*. The smoothing function of elevation (blue line) and its 95% CI (grey band) are added when the relationship is supported by GAMs (see Tables S3, S4, and S6). Black dots: observed values. Bimesters were defined according to the weather variability in our study site and the biological cycle of female chamois (colder months: November-December, January-February and March-April; warmer months: May-June, July-August and September-October).

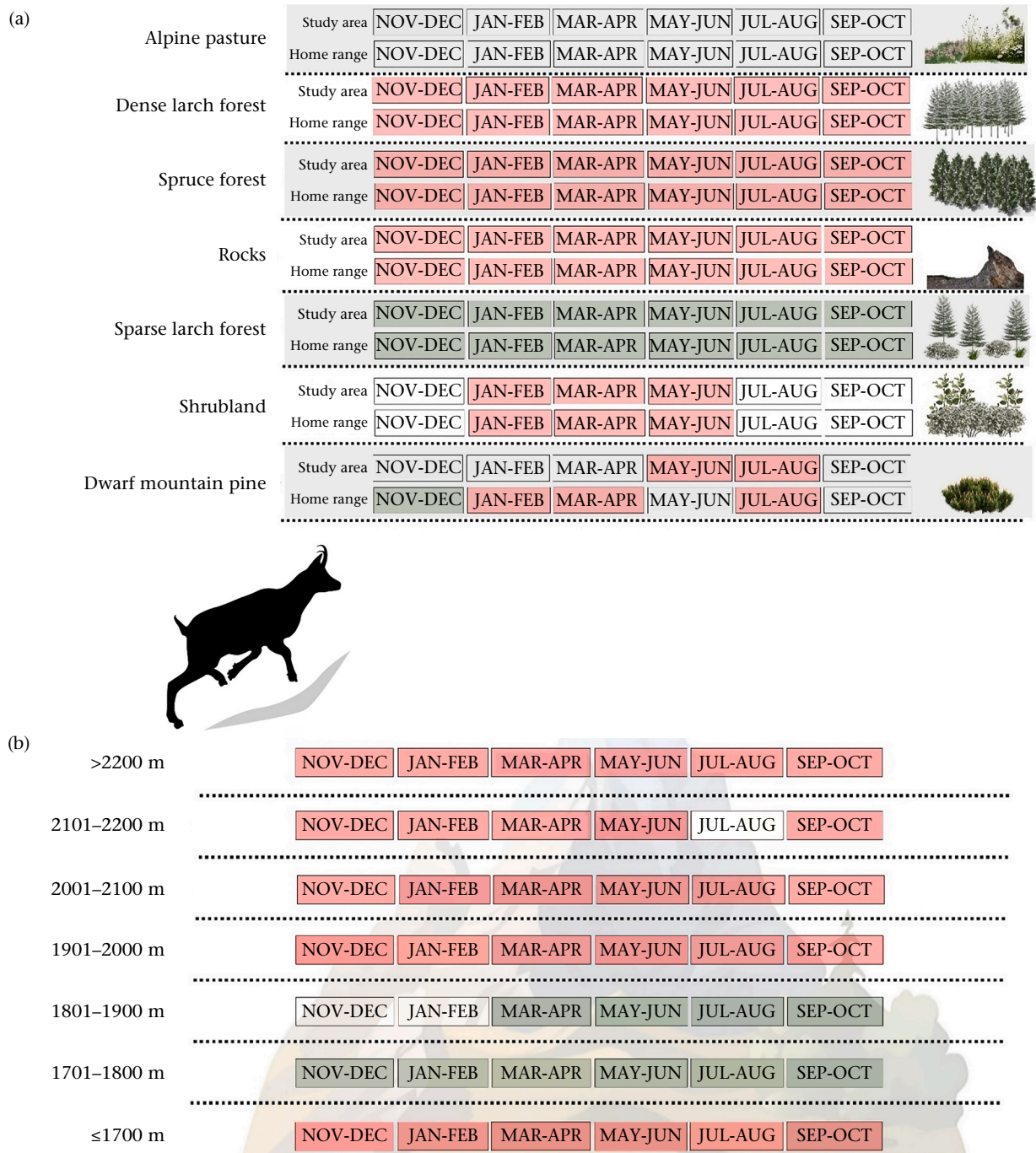
changed their summer locations differently according to environmental variables (Fig. 5c–f). Male sightings increased on steeper terrain, whereas females did not (Table S10; Fig. 5d). Conversely, on average, females appear to have increased the use of sites at higher elevations by moving >50 m upslope (89.4%; Table S10; Fig. 5c), although a minority of them moved to lower elevations or did not shift their locations in respect to 2000–2001 (10.6%,  $N = 339$  female-group sightings; Fig. S1). Females also used rocky locations more often (Table S10; Fig. 5e) and also changed the aspect of the ground used by moving  $\sim 30^\circ$  along the southwest-southeast direction (Table S10; Fig. 5f). In contrast, males showed no significantly relevant change.

The average significant increase in elevation of female chamois was entirely due to that occurring in two out of the five blocks surveyed, where they moved  $\sim 85$ – $90$  m upslope. In two other

blocks, no elevational change occurred, while in the fifth block, sightings of female groups were made at lower elevations, although the low number of sightings may have determined the lack of statistical significance (Table S11; Fig. S1).

## DISCUSSION

Our study presents the first detailed analysis of home range size, as well as habitat and elevation selections, of a large group of radio-tagged female chamois, monitored for  $\sim 27$  months/ind., on average. It has also investigated the effect of the ongoing thermal anomaly on chamois terrain use, thus providing a novel contribution to the understanding of the spatial dynamics of this mountain herbivore. The spatial behaviour of the female sex has been for long disregarded in behavioural studies (e.g. Rosenqvist

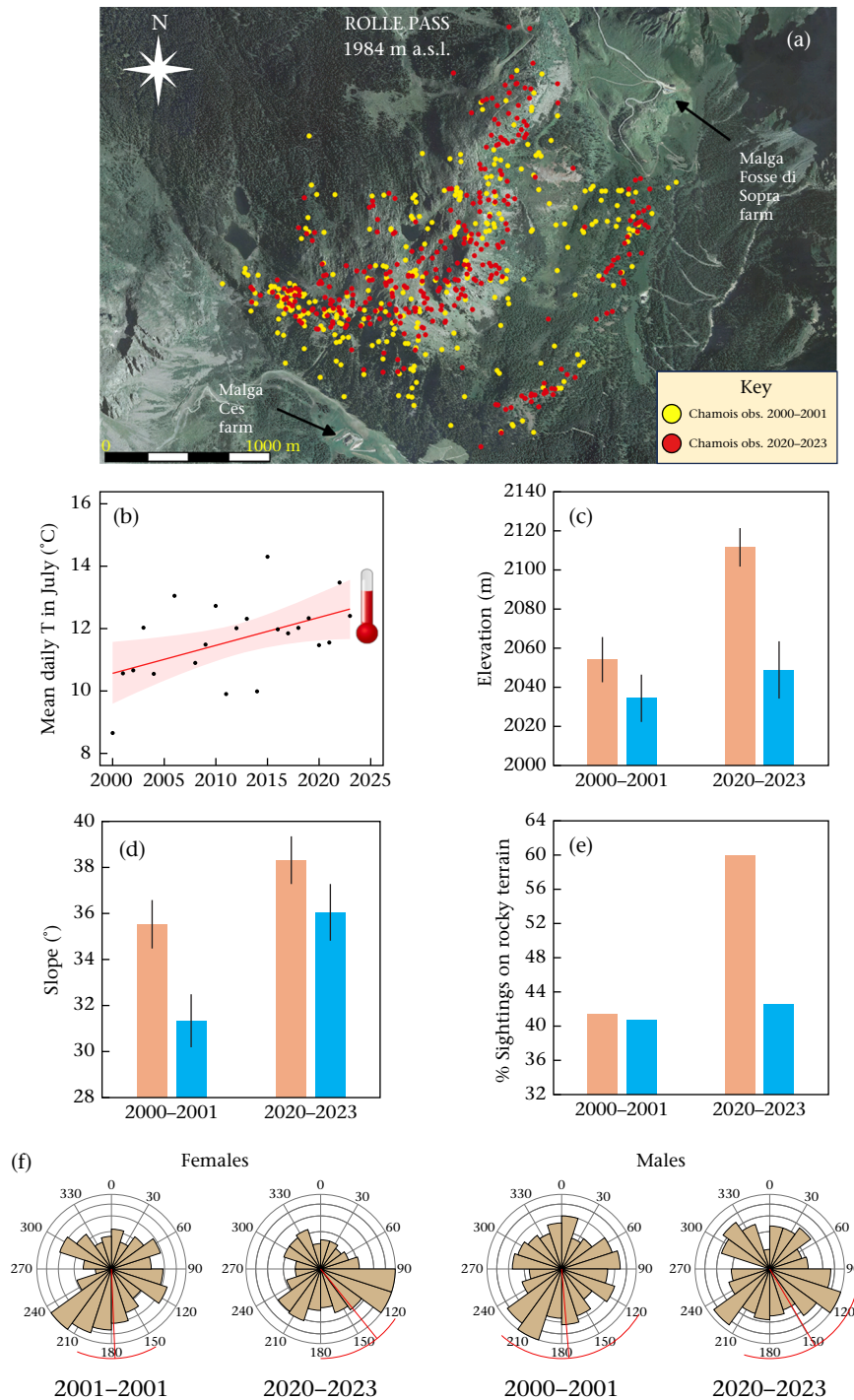


**Figure 4.** Selection by female radio-tagged chamois, *Rupicapra rupicapra* of (a) habitat types (study area: second order; home range: third order) and (b) elevational belts. Red: avoided; green: selected; white: proportionally used. For values of use and availability, see Table S8 (habitat types) and Table S9 (elevational belts), Supplementary Material. Bimesters were defined according to the weather variability in our study site and the biological cycle of female chamois (colder months: November–December, January–February and March–April; warmer months: May–June, July–August and September–October).

and Berglund, 1992; Wang et al., 2024). This fact is difficult to explain because females bear the greater investment for reproduction by producing eggs and their distribution influences the spatial behaviour of males (Isvaran, 2005). In mammals, females also undergo pregnancy, as well as suckling and protecting offspring to subadulthood.

Home range sizes of mountain ungulates depend mainly on the spatial distribution and quality of food resources (e.g. Brambilla et al., 2006; Michaud et al., 2024). Our radio-tagged females

showed smaller annual and bimonthly home range and core area sizes compared to other chamois populations (Clarke & Henderson, 1984; Hamr, 1985; Krämer, 1969; Unterthiner et al., 2012; cf. Table 1), which might be due to the high local forest/grassland productivity (Forti et al., 2025; Guastella, 2001). Contrary to our prediction that home range size would be smaller in colder months (prediction 2), the home range size of female chamois was smaller during the warmer months. On alpine meadows, the greater concentration and quality of vegetation patches in spring-



**Figure 5.** (a) Satellite map of the study area, with locations of sightings of chamois, *Rupicapra rupicapra* groups during standardized counts in July, 2000–2001 (male-group sightings:  $N = 140$ ; female-group sightings:  $N = 164$ ) and from 2020 to 2023 (male-group sightings:  $N = 127$ ; female-group sightings:  $N = 175$ ); a majority of sightings on ridges can be detected in the 2020–2023 count; see also Fig. 5c. (b) Changes in mean July temperatures in 2000–2023 (dots: observed values; line and band: predicted values and 95% CI). Differences in (c) mean elevation, (d) mean slope, and (e) use of rocky locations, between 2000–2001 and 2020–2023, for male (blue bars) and female (orange bars) groups of chamois (error bar: SE). (f) Differences in mean aspect (from the north direction), between 2000–2001 and 2020–2023, for male (right) and female (left) groups of chamois (red arrow: circular mean and dispersion). For statistical analyses, see Supplementary Material.

summer may serve as an attraction for chamois, reducing ranging movements in search of alternative food patches (Ferrari et al., 1988; von Elsner-Schack, 1985). For female chamois, suitable wintering areas should be steep enough to prevent high accumulation of snow, tend to be small, and thus female chamois generally move little from such areas (Hamr, 1985; Krämer, 1969).

The suitability of a wintering range for chamois can vary depending on local snow depth and wind direction (Anderwald et al., 2024), which may have prompted females in our study valley to move from one area to another, resulting in larger home ranges in the colder months. Females of the same herd should exhibit relatively uniform spatial behaviour (Conradt & Roper,

2000; Duranton & Gaunet, 2016). In contrast to our prediction 3, we observed high interindividual variability of home range and core area sizes within the same herd, independently of season. We also observed only moderate interindividual overlap in home ranges (~50%) compared with what may be expected for individuals belonging to the same herd (Del Mar Delgado et al., 2018). Most likely, this behaviour reflects the requirement of females to locate optimal foraging and birthing sites as the birth season gets closer (Duparc et al., 2019; Unterthiner et al., 2012). During the warmer months, the home range size of females decreased with increasing elevation, which may be explained by the conical shape of most alpine mountains, where available foraging areas decrease with elevation and rocky outcrops become prevalent (Semenzato et al., 2021; White et al., 2018). We cannot confirm the significant influence of kids on the home range size of lactating females, as reported for the alpine ibex, *Capra ibex* (Grignolio et al., 2007). In chamois, the young of the year are highly mobile and begin following their mothers shortly after birth (Krämer, 1969; Mikolas et al., 2013). Moreover, some 10–20 days after birth, when mothers have regrouped together, chamois display 'kindergarten' behaviour, in which females take turns to look after the young, whereas the other mothers go foraging (Ruckstuhl & Ingold, 1998).

In contrast with our prediction that alpine pastures would be avoided in the cold months because of snow cover (prediction 1), nutritious pastures at the highest elevations, i.e. alpine meadows, were used throughout the year proportionally to their local availability (cf. Unterthiner et al., 2012). Conversely, female chamois consistently selected sparse larch forests throughout our study period. This preference could depend on the mosaic of habitats within alpine forests, providing diverse foraging and cover opportunities (Knaus & Schroder, 1983, pp. 212–214; Unterthiner et al., 2012). Shrubland, rocks and other coniferous forests were avoided all year round, as they are usually poor in food resources (Duparc et al., 2019; Forsyth, 2000). The high cover that the alder shrubland provides (Guastella, 2001) was evenly used in summer and autumn for resting.

Long-term meteorological changes with increasing mean temperatures can negatively influence food availability and quality for mountain herbivores (Ferretti et al., 2018; Lovari et al., 2020; Pettorelli et al., 2007), decrease body growth (Reiner et al., 2021; Rugghetti & Festa-Bianchet, 2012), and reproductive success, in turn affecting population dynamics (Chirichella et al., 2021; Lovari et al., 2020; Pettorelli et al., 2007; White et al., 2018). Over two decades, July mean temperatures in our study area have increased by ~2 °C, at a rate of ~0.1 °C/year. Although comparing only two time periods, 20 years apart, may not permit inference of long-term trends or evolutionary adaptation, we suggest that the thermal change, presumably associated with a variation in food resources, could have been the primary driver of female movements upwards (Büntgen et al., 2017; Lovari et al., 2020), as they follow the pattern of increasing cold-adapted nutritious vegetation with elevation (Gottfried et al., 2012; Pauli et al., 2012; Stanisci et al., 2011). Compared with two decades earlier, male chamois did not show a comparable upward shift, but they are known to be ecologically more resilient than females as to food quality and security areas among cold-adapted ungulates (Ferrari et al., 1988; Rivrud et al., 2019). The analysis of bidecadal changes in slope aspects, besides revealing distinct patterns between sexes, supported the temperature-dependent hypothesis of alteration of food resources as triggering the change of chamois terrain use. Twenty years apart, most observations of females slightly moved from south-facing slopes to southeastern ones. In the northern hemisphere, south-facing slopes are the most exposed to sunlight in summer and

accumulate the highest temperatures (Auslander et al., 2003), which could decrease the quality of nutritious mountain vegetation (Dobrowski, 2011; Srivastava & Kumar, 2018) as well as heat stress, prompting female chamois to shift the aspect of their ranges (cf. Anderwald et al., 2024), besides the concomitant increase in elevation. Such south-northward movement may still be ongoing. In contrast, males showed no relevant changes in aspect between the two time periods, further suggesting that their movements are less limited by food constraints (Anderwald et al., 2024; but see Lovari et al., 2006; Unterthiner et al., 2012). Although we cannot discard increased interspecific competition with red deer (cf. Anderwald et al., 2016; Donini et al., 2021; Ferretti et al., 2015), approximately half of the hinds abandoned our study valley in the warmer months to come back in the colder ones (Bocci et al., 2010). In contrast, chamois remained within the study area throughout the year. This suggests that, despite a moderate upward shift in red deer distribution (e.g. a few dozen metres in elevation) over the past two decades, the degree of interspecific spatial overlap should not have increased (Bocci et al., 2010, 2012). Moreover, in the last two decades, the increased use of higher and rocky terrain by females might suggest a complementary role of recolonizing wolves to drive changes in chamois terrain use (cf. Orazi et al., 2025), which might also explain the increased use of steeper slopes by males (cf. Baruzzi et al., 2017). Thus, the arrival of the wolf might have been an additional factor in pushing females with kids to rocky cliffs, providing greater security, although just one pair of wolves formed in 2017 in our study area (Groff et al., 2018). Inevitably, our evaluation of bidecadal changes in chamois terrain use is not exempt from the limitation of comparing two specific periods in time. Although our data offer clues to understand differences occurring 20 years apart, they should be interpreted with some caution, and a complete time series spanning longer periods would be necessary to better shed light on ecological trends and potentially adaptive responses of chamois.

We expected little variation in the spatial movements of chamois females belonging to the same herd. Although we have no information on their movements in the intermediate period between 2000–2001 (period A) and 2020–2023 (period B), their distribution pattern did not appear to change homogeneously, not supporting our prediction 3 on a similar behaviour of female chamois belonging to the same herd. There was a mean increase in elevation of sighted chamois between period A and period B of >50 m upslope; even greater (i.e. ~90 m) if we eliminate the few female chamois moving downwards or not moving. The majority of female groups (89.4%) moved upwards in relation to 2000–2001, most likely searching for cooler temperatures and cold-adapted nutritious vegetation, whereas 10.6% of female groups did not, i.e. remained at the same elevation or even moved downwards (Fig. S1). Reactions of chamois to increasing temperatures have been reported as follows: (1) moving to higher elevations, if available, thus following the phenological progression of key plant associations (Anderwald et al., 2024; Büntgen et al., 2017) as well as avoiding heat stress (Mason et al., 2014; Semenzato et al., 2021); (2) moving to lower elevations (e.g. Herrero et al., 2023; Perco et al., 1997), presumably in search of new suitable cooler cover areas; (3) reaching near-extinction locally (Lovari et al., 2020). Our data suggest that not all individuals in a population or herd show the same response to environmental change. For example, Michaud et al. (2024) have reported two ecotype-related tactics of mountain goats, *Oreamnos americanus*, to cope with thermal stress. Our work has shown a high interindividual variability in female spatial behaviour, with more than 80% variability in home range size explained by individual identity. Although predation and interspecific competition

may have played ancillary roles, alteration in vegetation distribution, i.e. local food availability, was probably the major factor triggering chamois movements (Thuiller et al., 2018). Despite belonging to the same herd, a few female chamois showed different spatial responses. This behavioural diversity may be adaptive to ensure survival in a changing environmental context, as natural selection can only take place if there is individual variation.

Our study provides novel insights into the spatial behaviour of a mountain mammal, suggesting that females, the key drivers of population dynamics, can manifest a substantial degree of behavioural diversity even among members of the same herd. Furthermore, our study has revealed variability in behavioural responses to environmental changes. Over the Pleistocene, no less than 100 major (>300 years each) glaciations and interglacials have impacted population movements of mountain ungulates (Crawford, 2014; Lovari, Sforzi, & Mori, 2013). Thus, we can assume that extant species are adapted to deal with a variety of alternative solutions to environmental changes, or they should have gone extinct, emphasizing the evolutionary resilience and historical adaptability of mountain ungulates. Recently, it has been suggested that a mountain-dwelling large mammal may use its eyesight to scan the landscape and decide where to disperse, even crossing long stretches of unsuitable terrain, provided the destination is in sight (Johansson et al., 2024), which may suggest an additional explanation for differential dispersal behaviour. Of course, one should not expect that all solutions are equally successful and thus subpopulations may disappear to form again through recolonization, when the thermal change has regressed. Forests may act as a temporary cooler refuge habitat (Reiner et al., 2021), but even forests will be affected by a prolonged thermal stress lasting hundreds or thousands of years. Furthermore, forest expansion may exert additional challenges to mountain ungulates, such as changes in forage quality and availability, and promote predator occurrence. With respect to past climatic changes, the heavy habitat alteration caused by humans, especially between mountains (i.e. urbanization, Kati et al., 2020), is the only new critical factor militating against the colonization of some potential refuge areas for mountain ungulates, thus decreasing their odds of long-term survival.

### Author Contributions

**Sandro Lovari:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Conceptualization. **Niccolò Fattorini:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Chiara Luvie:** Writing – review & editing, Investigation. **Alessandra Tagliabò:** Writing – review & editing, Investigation. **Piergiorgio Partel:** Writing – review & editing, Resources, Data curation. **Silvia Bonat:** Writing – review & editing, Investigation. **Emiliano Mori:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization.

### Data Availability

The data used in this study are available as supplementary material.

### Declaration of Interest

The authors have no competing interests.

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### Supplementary Material

Supplementary material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2025.123446>.

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